

N. Bancroft

A Review of Literature
Concerning the Evolution of
Monocotyledons

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CONCERNING THE
EVOLUTION OF MONOCOTYLEDONS.

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N. BANCROFT.

[WITH FOUR DIAGRAMS IN THE TEXT.]

[NEW PHYTOLOGIST REPRINT, No. 9.]

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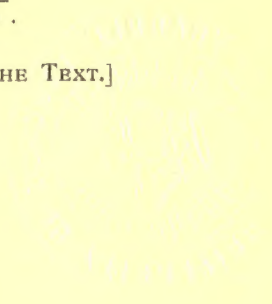
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BY N. BANCROFT.

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I. INTRODUCTION.

WHAT is the position of Monocotyledons in a natural system of classification—that is, a system which takes into account the probable evolution of the group and its relationship to other forms? This is a question of considerable interest, and one which has given rise, particularly of late, to various theories of the primitive or derived nature of monocotily, and to many phylogenetic schemes.

II. OLDER CLASSIFICATIONS AND VIEWS OF THE POSITION OF THE GROUP.

John Ray (55), whose "Historia Plantarum" was published between 1686 and 1704, was the first systematist to base his classification of flowering plants on the presence of one or two cotyledons in the embryo. This character provided a convenient method of grouping, and has been used by the majority of writers since Ray's time. It is very possible, that in framing their systems of classification, even the earliest botanists had some underlying ideas of *degree* of development (though not necessarily of phylogenetic or evolutionary development), and also of relationship between their plant-groups; and it is therefore interesting to note that in the majority of cases since Ray's time, Monocotyledons are placed *before* Dicotyledons, or between that group and the flowerless plants.

(42), Warming (74) and Hallier (26, 27, 28). These may be considered briefly with regard to their treatment of the two main divisions of the Angiosperms.

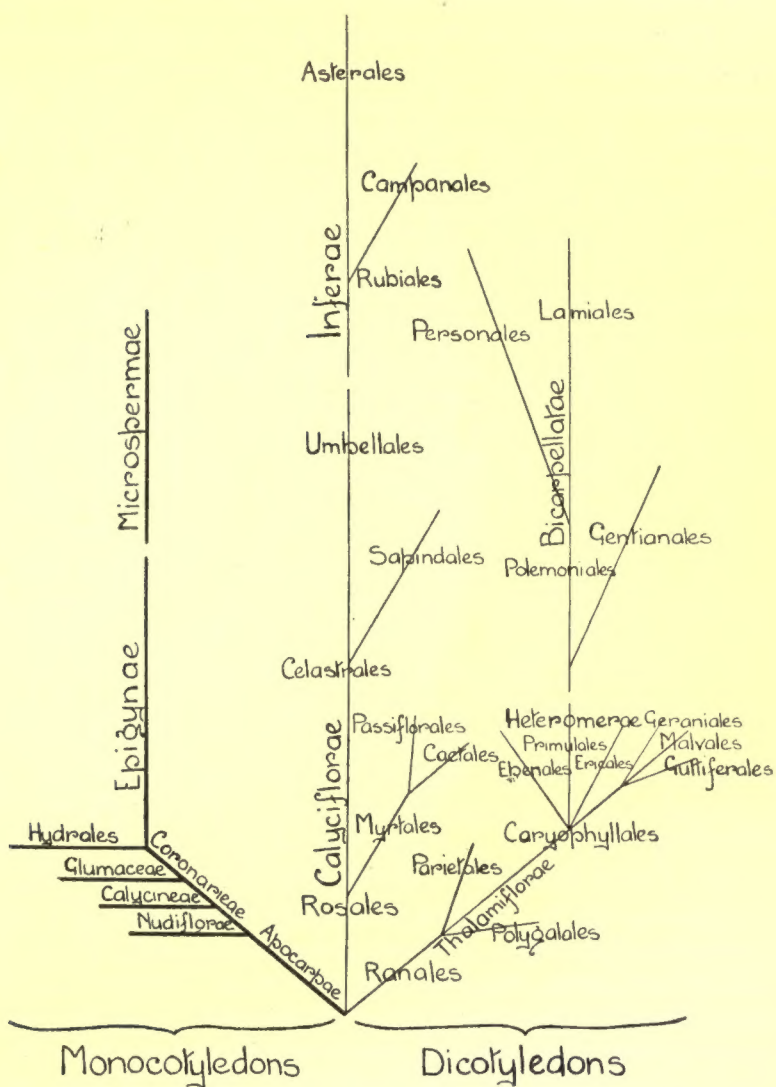


DIAGRAM II.

The Evolution of the Monocotyledons according to Bessey's System (1897).

Bessey (Diagram II; see 7) considers that Monocotyledons and Dicotyledons are modifications of a common type, diverging from one another at an early period, the apocarpous forms of both

groups being the most nearly related.¹ There is no evidence that either group was derived from the other, but there are, according to Bessey, structural indications that Monocotyledons must rank lower than Dicotyledons. He believes that the earliest forms of both groups made their appearance almost simultaneously in late Permo-Carboniferous or early Mesozoic times, but palæobotanical investigations show that there is no actual reliable evidence for the presence of Angiosperms before the Cretaceous,² though both subgroups appear to be well-established by the end of that period, according to the work of Drs. Stopes and Fujii (67, 68). A recent paper by Horwood (36) gives a useful summary of fossil Monocotyledons, showing that the first authentic specimens are from the Cretaceous. Horwood agrees with Bessey in believing that Monocotyledons and Dicotyledons arose from a common ancestor, resembling an Alismaceous or Liliaceous type on the one hand and a Ranalean type on the other.

Engler (21) deals with the Monocotyledons before the Dicotyledons, explaining that he leaves them in the position they have generally held in previous classifications, because he does not consider that there is sufficient evidence for the growing idea of their derivation from Dicotyledons. He prefers to regard them as two groups of equal value (21, p. vi of preface). Of the phylogeny of the Angiosperms as a whole, he gives very little idea, but considers both Monocotyledons and Dicotyledons as being polyphyletic (20, pp. 371-380).

Warming (74) also places the Monocotyledons first in his system, and follows Engler in preferring, in the present state of our knowledge, to consider Monocotyledons and Dicotyledons as two independent lines of evolution.

It may be remarked before passing on to other systems that this view of independence of the two groups was suggested as early as 1875 by Kny (37, p. 61). It was held by Drude (17, pp. 184, 304) and has had various supporters who have set forth their ideas of phylogeny more or less definitely. For example, Coulter and Chamberlain (12, pp. 284, 285) derive the Monocotyledons from an *Isoëtes*-like ancestor, and the Dicotyledons from a *Selaginella*-like type on the grounds of similarity of the embryos. As an alternative they suggest that both came from extinct lines of Eusporangiate

¹ Cf. Fritsch (23). This author believes that the Ranales and Helobieæ had a common origin in extinct and unknown forms.

² Cf. Scott (64, p. 660); Seward (65, p. 220); Coulter and Chamberlain (12, p. 273).

Heterosporous Filicales.¹ Fritsch (23) considers Monocotyledons and Dicotyledons to be two independent groups having evolved from a common ancestor, extinct and unknown, by way of the Helobiae and Ranales respectively, or having had separate origins in extinct Gymnosperms or Pteridophyta. Lindinger (40; see also 39), in 1910, has been one of the most recent exponents of the "independence theory." From a consideration of root and stem-structure in Monocotyledons, he concludes that this line is independent so far

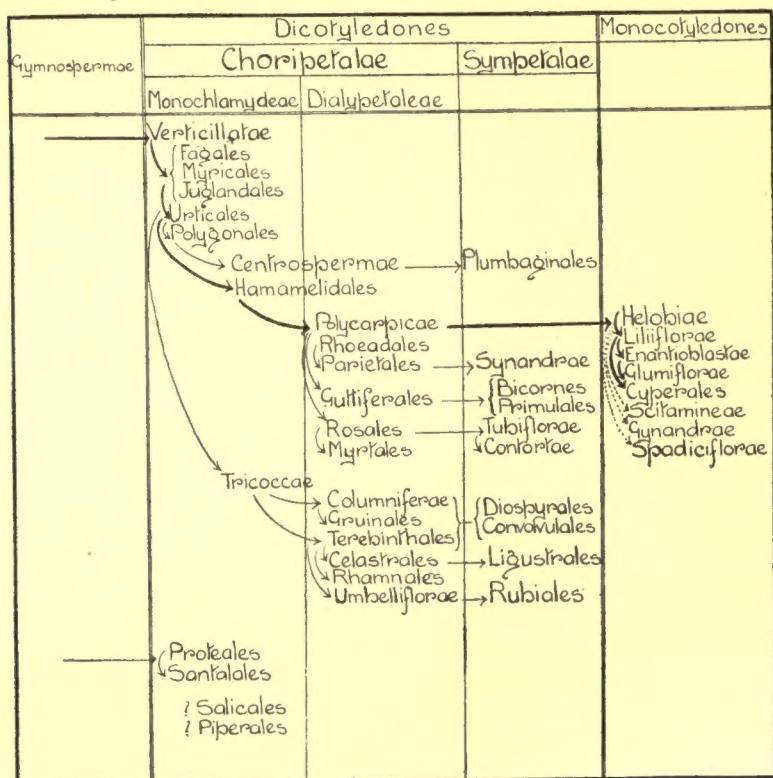


DIAGRAM III.

The Evolution of the Monocotyledons, according to Wettstein's System (1911).

as the Dicotyledons are concerned; nor can any connection be traced with known Gymnospermous types, recent or fossil. In considering the characters of the primitive Monocotyledon, Lindinger mentions *Dracaena*, *Aloë* and *Yucca* as having retained ancestral characters in the purest form—an interesting point in connection

¹ They admit, however, that "the arguments in favour of the monophyletic origin of Angiosperms are strong; and if this view be accepted, the derivation of Monocotyledons from primitive Dicotyledons seems to rest on stronger evidence than the reverse relationship" (p. 288).

with the idea of the primitiveness of the arboreal habit (cf. 5, 10, 18). He contends that while the Angiospermous condition may be regarded as an argument for intimate relationship between the two groups, this condition may have arisen more than once, in the same way as did the seed-habit.

According to Wettstein (75, p. 865), the Angiosperms are monophyletic, or possibly diphyletic (Diagram III). The chief point of his system in the present connection is that he derives all the Monocotyledons through the Helobieæ from the Polycarpicæ (a group corresponding broadly to Engler's Ranales). The Polycarpicæ in their turn he considers as having descended from Gymnosperms by way of the Monochlamydeæ, as the diagram shows.

Lotsy (42, pp. 863, 864) also believes that the Dicotyledons are the older type (Diagram IV), but he derives the Monocotyledons from them at two different points—the first in the neighbourhood of the Piperales, through which the Spadicifloræ are considered to have evolved; and the second in a hypothetical group, the Proranales, from which lines of evolution are traced to the Liliifloræ and Helobieæ. A similar diphyletic view of the origin of Monocotyledons was suggested by Hill in 1906, in a paper on Piperalean seedling-structure (33, pp. 173, 174). According to Lotsy, the whole of the Angiosperm phylum is derived from the Bennettiteæ by way of a hypothetical Proangiosperm ancestor.¹

Hallier (26, 27, 28) has advanced a system which he varies in different degrees from time to time—as Lotsy remarks, it is free from the reproach of being too rigid. In all his variations, however, he treats the Dicotyledons as the older form and derives them from Cycadophyte ancestors. The Monocotyledons he refers to ancestors amongst the Polycarpicæ, which group he gives thirty-two reasons for considering as primitive.

With regard to the primitiveness of the Polycarpicæ and their relation to the Monocotyledons, the following investigations are of interest. Fries (22) in studying the leaf-arrangement on lateral axes, found that among the Anonaceæ and Nymphæaceæ, the Monocotyledon type, in which the first leaf is adaxial to the main axis, is more common than the Dicotyledon type, in which the two first leaves are transversely placed (see 22, fig. 1, p. 294). Mez and Gohlke (48), from serological investigations, decide that the Magnoliaceæ include the most primitive Angiosperms, and that the Alismataceæ, Butomaceæ and Juncaginaceæ are primitive among Monocotyledons.

¹ Cf. Arber and Parkin (2) and Hallier (27).

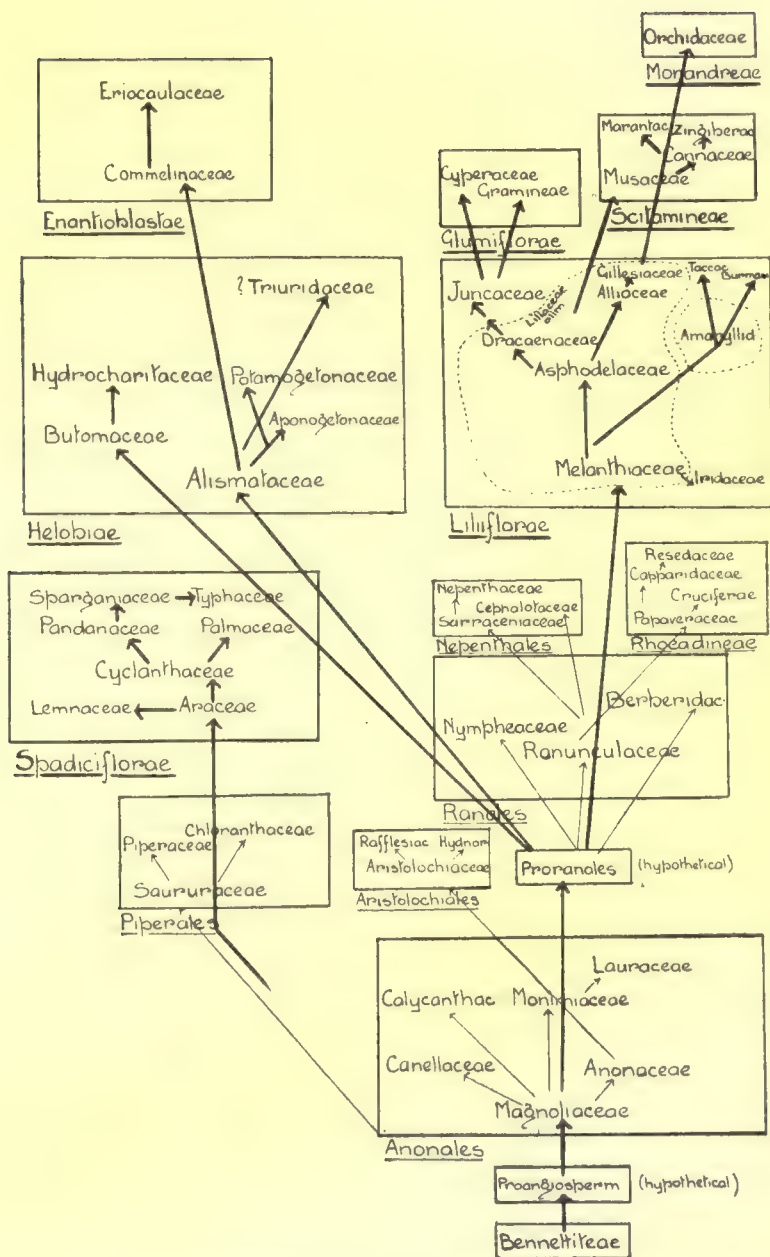


DIAGRAM IV.
The Evolution of the Monocotyledons, according to Lotsy's System (1911).

Alisma reacts serologically to *Magnolia*, thus showing, according to Mez and Gohlke, direct relationship between the two forms.¹ Maneval (47) has recently studied the development of *Magnolia* and *Liriodendron*, and concludes that the Magnoliaceæ or related forms represent the most primitive of existing Angiosperms. Porsch (54, p. 589) sees in the floral nectary a valuable phyletic character giving further support to the view that Monocotyledons have been derived from Dicotyledons through such forms as the Polycarpicæ. Finally, in a study of the development of *Butomus umbellatus*, Holmgren (35) draws attention to the frequent formation of several-celled archesporia in this species, and notes similar formations in the Ranunculaceæ. He does not insist too strongly upon the point, however, as many-celled archesporia are found in widely different plants.

Although the majority of botanists have now been led to regard Dicotyledons as representing the primitive stock—or at least to take up a non-committal attitude—one or two writers still believe, on anatomical grounds, that Monocotyledons are the more primitive and themselves gave rise to Dicotyledons by the splitting of the one original and primitive cotyledon. One of the chief supporters of this theory is Lyon (44, 45, 46) whose work on *Nelumbium* convinced him that in this form the development of two cotyledons may be traced through the division of a single terminal member, homologous with the single seed-leaf of Monocotyledons, which are to be derived directly from a primitive monocotyledonous Angiosperm stock. In order to account for the terminal position of this cotyledon, he suggests that it is not a phyllome, but an organ *sui generis*, comparable with the foot of Vascular Cryptogams, or with the sucker in *Gnetum* or *Welwitschia*. Lyon's theory of the primitiveness of Monocotyledons and their production of a dicotylar race need not be considered further, for it has not received any consistent explanation, nor are the anatomical (and other) differences between the two classes accounted for (cf. Sargent, 62, p. 175).

It may be safely concluded that on the whole, opinion at present inclines strongly towards the view that Monocotyledons have been derived from a dicotyledonous stock—a view suggested by Strasburger (69, pp. 317, 318) as long ago as 1872. Miss Sargent (57-62) has been largely responsible for the advancement of the theory,² and the work of other botanists, along similar or different lines from those followed by Miss Sargent, has contributed to its support.

¹ Stuchlik (70) gives a long list of references on the subject of Botanical Serology.

² Cf. Moss (51, p. 207).

IV. THE PROBABLE MANNER OF EVOLUTION OF THE MONOCOTYLEDONS FROM A DICOTYLEDONOUS STOCK.

If it is agreed that Monocotyledons have evolved from a dicotyledonous ancestry, a further problem presents itself, concerning the *manner* of their evolution from the parent stock, and the *cause* of their breaking away from it. Here again, considerable difference of opinion is encountered, and in this case, the differences appear to be increasing rather than decreasing.

The main issue depends upon the solution of the problem with regard to the derivation of the condition of monocotily from the condition of dicotily.

As Lotsy (42, p. 624) points out, there are various means by which this may have been accomplished, and these may be grouped under the headings of Syncotily and Heterocotily. It is proposed to treat these two processes separately giving as far as possible their probable causes.

1. Syncotily. Syncotily—or the fusion of the two cotyledons to form one member—has its chief exponent in Miss Sargent (57-62), whose anatomical investigations have convinced her that the vascular symmetry of monocotyledonous seedlings may be directly or indirectly referred to the same type as that of dicotyledonous seedlings in which fusion of the cotyledons has plainly taken place. Before proceeding to a special consideration of syncotily, it may be well, perhaps, briefly to summarise Miss Sargent's conception of the Primitive Angiosperm from which she derives Monocotyledons. This author accepts Arber and Parkin's idea of the evolution of the Angiosperms (2 and 3), and derives both Monocotyledons and Dicotyledons from a race of primitive Angiosperms which she would place below the Ranalean plexus in Arber and Parkin's table (see 2, p. 77). Primitive Angiosperms possessed characteristics common to both the modern sub-groups: namely, secondary growth by means of a cambium; flowers of Ranalean type, Arber and Parkin's idea of the evolution of the angiospermous flower being accepted (2, figs 1, 2 and 4); closed carpels; endosperm; two cotyledons; and seedlings with tetrach vascular symmetry.¹ Primitive Angiosperm having two cotyledons, it is necessary to find a means of determining how the descendants along one line might come to possess only one. It is almost impossible to determine this from a study of the development of the young embryo within

¹ For views on the primitiveness (or otherwise) of tetrarchy see Tansley and Thomas (72), Thomas (73), Compton (10), Hill and de Fraigne (34); see also Tansley's criticism of Miss Sargent's theory (71).

the embryo-sac. The case of such psuedomonocotyledons as *Ranunculus Ficaria*,¹ *Corydalis cava* and *Carum Bulbocastanum* illustrates this point. Resort is therefore made to the evidence of comparative seedling anatomy.

Very generally, in the seed-leaf of Monocotyledons, a true midrib is replaced by two equal bundles. In some forms these bundles are so arranged as to suggest that each represents the midrib of an ancestral cotyledon, and a comparison of certain monocotyledonous seedlings, such as *Anemarrhena*, with those of some Ranalean forms (for example, *Eranthis hiemalis*) supports this suggestion (58, p. 109; Pl. II). The *Anemarrhena* seedling anatomy may be taken as a primitive type, since it leads by intermediate forms through at least four lines within the Liliaceæ. It may be described shortly as follows (57, 58, p. 109; Pl. II, figs 1-6):—

The cotyledon of an *Anemarrhena* seedling is somewhat flattened, and the plumule is rather late in development. In the example figured by Miss Sargent, it is still completely enclosed within the base of the cotyledon. The axis, which is somewhat thickened immediately below the plumule, passes at once into the strongly developed primary root. The vascular system of this seedling is symmetrical, two large bundles running the whole length of the cotyledon, which is elliptical in transverse section. Towards the base of the cotyledon, the two bundles are slightly displaced from their hitherto symmetrical position by the formation and growth of the plumule; but although this displacement extends into the transition region, the transition itself takes place in a symmetrical manner. Three branches of protoxylem are derived from each xylem group, and each phloem group divides into two. The lateral branches of protoxylem fuse in pairs, and the result is a tetrarch root-stele.

In certain Dicotyledons, the seed-leaves are normally united to a greater or less degree, sometimes by one margin only, but more often by both. In the latter case the united petioles form a tube, sometimes of considerable length (see Sargent, 59; Table I, pp. 73, 74). Petiolar tubes of this kind are found in a good many of the Ranunculaceæ and in other orders; and in all investigated cases, they are accompanied by a much shortened and thickened hypocotyl.

¹ In this species the evidence from embryogeny has led Sterckx (66) to assume that monocotylly has arisen by fusion of two cotyledons; Hegelmaier (29) and Schmid (63), on the contrary, think that suppression of one cotyledon has taken place

The anatomical structure of the petiolar tube and thickened hypocotyl of *Eranthis hiemalis*—one of the Ranunculaceæ—recalls that of an *Anemarrhena* seedling. In the *Eranthis* seedling figured by Miss Sargent (58, Pl. II, figs. 7-12), the blades of the cotyledons alone are separate, the petioles being united throughout their whole length to form a slender cylinder. This cylinder is solid just below the blades and above the stem-bud, but hollow between these levels, and hollow again over the tuber on which the stem-bud is developed. Three bundles from each cotyledonary blade enter the cylinder, but the two lateral traces from each blade rapidly unite with their own midrib, so that the petiolar cylinder contains two bundles each representing a separate cotyledon. The section passing through the stem-bud shows each bundle dividing into two, and finally there are formed in the hypocotyl four bundles of stem-type, arranged more or less in pairs. As these bundles become more widely separated with the increasing girth of the hypocotyl, three, and ultimately four xylem groups are formed, corresponding to each pair of phloem groups. As the hypocotyl narrows again towards its base, the xylem collects into four masses, and the four phloem groups fuse in pairs. A diarch root-stele is formed by the disappearance of two of the protoxylem groups.

In spite of the differences in detail, the resemblances between *Anemarrhena* and *Eranthis* are sufficiently clear to suggest that each may be referred to the same dicotyledonous plan.

Zygadenus elegans, a species belonging to the same family as *Anemarrhena*—Liliaceæ—has seedlings exhibiting unilateral vascular symmetry, with one cotyledonary bundle. This type may be connected with the *Anemarrhena* type, however, by intermediate forms; and Miss Sargent finds that seedlings from other monocotyledonous families may be derived from a Liliaceous type, or shown to be similarly bisymmetrical.

In these bisymmetrical cases, fusion of the two original cotyledons may be supposed to have taken place by both margins, as clearly indicated in the case of *Eranthis* and other Dicotyledons, where a cotyledonary tube is formed. Miss Sargent further states that monocotly may arise by fusion of the cotyledonary petioles by one margin only. She quotes the cases of *Ranunculus Ficaria*¹ and *Anemone apennina*,² conceiving these to be well-proved cases of the

¹ Cf. the view of Hegelmaier (29) and of Schmid (63), that monocotly in this species is due to suppression of a cotyledon. Compton (11, p. 802) thinks that "on the whole the tendency of the evidence seems to be in favour of the view that the seed-leaf of *R. Ficaria* represents a single cotyledon."

² Compton (11, p. 802) thinks there is some doubt about this species.

normal fusion of cotyledons by one margin only, and adds that fusions are not infrequently found in abnormal specimens of types having distinct cotyledons (59, p. 75), such as *Ranunculus repens*, *Ranunculus chius* and *Urtica dioica*. These instances suggest that the single seed-leaf of some other species of pseudomonocotyledonous Dicotyledons may have been formed in a similar way (see Sargent, 59, Table II, p. 76, 77),¹ and, of course, indicate the possibility of a similar origin of monocotly in true Monocotyledons.

Miss Sargent next considers the apparently terminal position of the single cotyledon in Monocotyledons, maintaining that if it "be derived from the two cotyledons of an ancestor, it cannot really be terminal, but must represent the congenital fusion of two lateral members" (60, p. 339). In the case of *Delphinium nudicaule* (60, p. 339, figs. 1 and 2), which possesses a cotyledonary tube, the first leaf breaks through the tube near its base, and for some time appears as though laterally inserted on the cotyledonary axis. But as the leafy stem develops, the cotyledons are pushed aside and assume their true position as lateral organs. In the case of congenitally united cotyledons, a lateral position of the stem-bud is necessary to free development. The cotyledons are usually formed some time before the growing point of the stem, and naturally, the single rudiment which represents both cotyledons tends to lie in a straight line with the suspensor and future axis. Thus, when later the plumule is developed, it must take up a lateral position (see 60; p. 340, fig. 3, *Alisma*), and only attains its true terminal position after germination, when it pushes the cotyledonary member aside. *Tamus* (60, fig. 6) and *Commelina*, however, are examples in which the growing point is terminal and the cotyledon lateral from the first. *Corydalis cava* has a single cotyledon like that of *Tamus* in form and position (60, cf. figs. 4 and 5 with fig. 6); and the simplest explanation of both cases is that the single cotyledon represents "the fusion of two ancestral cotyledons, but that on account of the early formation of the rudimentary plumule, or perhaps because the cotyledons have united by one margin only . . . the stem-bud has never lost its terminal position" (60, p. 340).

This view of the monocotyledonous embryo overcomes the difficulties of regarding the single cotyledon as a terminal leaf, or as in the case of *Nelumbium*, according to Lyon, as an organ of an entirely different nature.

Miss Sargent's next point in her very complete and consistent theory, is a consideration of the causes and advantages of cotyle-

¹ Cf. Compton (11, p. 803, footnote 3).

donary fusion. The large number of Dicotyledons exhibiting cotyledonary fusion indicates that it does offer advantages under certain conditions.

What these conditions are is indicated at once by the fact that cotyledonary fusion is accompanied in practically all cases by shortened and thickened hypocotyls¹ (as in *Eranthis*), and by the formation of underground storage organs of some kind. The plants possessing these characteristics are geophytes, that is, plants whose aerial organs persist for a short annual season only, the underground parts forming a storage of food materials through the dead season (cf. Areschoug, 4, p. 1). The fact that most Dicotyledons exhibiting cotyledonary tubes are highly specialised geophytes suggests that fusion of the cotyledons is an adaptation to this habit. A consideration of the conditions under which a typical geophyte lives—for example, in Arctic regions, or on Alpine summits—makes it evident that its seedlings must be exceptionally well-adapted to their environment in order to survive. By the end of the short period of growth the young seedling must be in a condition which will enable it to live during the adverse weather following; so that at the commencement of the vegetation season it begins at once to form its underground organs.² “In all cases however, the production of assimilating surfaces seems to be an object of secondary importance” and “concurrent cotyledons may be regarded as an adaptation for producing effective assimilating surfaces with the least possible expenditure of material. The production of a single cotyledon, whether by the more complete fusion of two or in any other way, is also an economy as compared with the formation of two cotyledons” (59, p. 80).

After a consideration of the above facts, Miss Sargent concludes that Monocotyledons have evolved through adaptation to a geophilous habit, an indication as to how this may have taken place being given by certain geophilous Dicotyledons which possess a single cotyledonary member. Many of the distinguishing features between Monocotyle-

¹ The correlation of cotyledonary tubes and thickened hypocotyls has been noted by Sterckx (66, pp. 80, 81), Lord Avebury (Lubbock, 43, II, pp. 23, 24) and Darwin (13, p. 97).

² The behaviour of geophilous seedlings during the first season of growth falls into four classes:—

- i. The whole structure may remain underground—*Megarrhiza californica* and *Arum maculatum*.
- ii. The cotyledons only appear above ground—*Eranthis hiemalis* and *Fritillaria imperialis*. This is the most usual behaviour.
- iii. The cotyledons may remain underground in the seed, and the first leaf break through the soil—*Anemone nemorosa* and *Eucomis nana*.
- iv. Both cotyledons and foliage leaves come up above ground and act as assimilating organs—*Delphinium nudicaule*.

dons and true Dicotyledons may be explained as having arisen as a result of such adaptation; for example, the presence of endosperm in the seed of most Monocotyledons is a character of highly specialised geophytes; the distribution of vascular bundles in the stem and the loss of cambium in Monocotyledons may be ascribed to the shortening and thickening of the axis; the disappearance of the primary root and development of an annual crop of adventitious roots are clearly connected with the annual recurrence of a period of vegetative activity; the form and venation of monocotyledonous leaves are the most suitable for insertion on the shortened axis and also for pushing up through the soil. The absence of a true epidermis on the root above the root-sheath¹ and the trimerous symmetry of the flower in Monocotyledons are points less easy of explanation, but in most respects, Miss Sargent's theory is exceedingly well supported and shows that there is much to be said for the origin of Monocotyledons from a dicotyledonous race by Syncotyly, certain Liliaceæ being considered to give the key to the situation.²

Compton (11, p. 800) from a study of teratological syncotyls amongst Dicotyledons, concludes that leaving the Spadicifloræ out of the question, syncotyly may well account for the origin of monocotyly in other Monocotyldons.³ He adds the following valuable observations to those of Miss Sargent:—With very few exceptions (*Serratula radiata*, *Limnanthes Douglasii*, *Cardamine* spp. and possibly *Megarrhiza californica* (cf. Sargent 59, p. 83), species forming a cotyledonary tube have albuminous seeds, so that the small and usually straight embryo develops in a homogeneous medium, the endosperm. If syncotyly occurred at all, it would be expected to be symmetrical under these conditions—that is, to affect both edges of the cotyledons equally. On the other hand, species which are normally dicotyledonous but which occasionally produce syncotyls, are mostly exalbuminous, the exceptions being about one

¹ Cf. Henslow (31, p. 732). This author ascribes the absence of an epidermis to the degenerating influence of a moist or aquatic habit.

² With regard to the primitiveness of the Liliaceæ, see also Lindinger (40), Lotsy (42), Hallier (28). Miss Sargent believes that aquatic Monocotyledons, such as the Helobieæ, may be explained as having taken to an aquatic habitat in order to escape competition with the better-equipped Dicotyledons on land; their characters must be regarded as secondary rather than primitive. Bessey, Wettstein and Warming, on the other hand, consider the apocarpous Helobieæ to be the most primitive of Monocotyledons, a view indicated by Hallier in 1905 (27); Lotsy also admits the claims of the group to primitiveness, deriving them from Pro-ranalean ancestors in common with the Liliifloræ. Nicotra (52) holds that the Cyclanthaceæ are the primitive Monocotyledons.

³ In this connection, it is interesting to note that Mottier (50) concludes, from his work on anomalous Dicotyledons, that the facts of their embryology "throw little or no light upon the relative antiquity of the two classes of Angiosperms" (p. 460).

in six. Amongst Monocotyledons, the Helobieæ are exalbuminous, and the embryos of this group possess unilateral symmetry, suggesting that syncotyly has taken place along one edge of the cotyledonary petioles. Assuming, as Compton does, the primitiveness of the Helobieæ, it seems as if unilateral symmetry must be primitive for Monocotyledons, rather than the Liliaceous bilateral symmetry, according to Miss Sargent. The alternative is to suppose, with Lotsy (see Diagram IV), that the Helobieæ and Liliifloræ are two independent lines from a common stock; the first line may have adopted asymmetrical syncotyly, having originated in an ancestor with exalbuminous seeds, while the second, descending from an albuminous type, became symmetrically syncotylous.

2. **Heterocotyly.** Heterocotyly, according to Lotsy (42, p. 624), may be of different kinds. Firstly, there may be a division of labour between the cotyledons, one remaining in the seed and becoming a suctorial organ, and the other escaping and forming the first assimilatory organ.

This view is well illustrated by certain geophilous species of *Peperomia* described by A. W. Hill in 1906 (32; figs. 1-9, p. 420). In this genus a series may be traced from species which are truly dicotyledonous—for example, *Peperomia pellucida*—to species in which there is a monocotyledonous club-shaped absorbing organ, from which all trace of its original leaf-like character has disappeared, as in *Peperomia parviflora*. *Peperomia peruviana* is an intermediate stage, both cotyledons having a distinctly leaf-like form, but one remaining within the seed and forming an absorbing organ, the other becoming the first aerial assimilating organ.

According to Hill, the cotyledon of some of the Araceæ and *Tamus communis* is closely comparable with the absorbing cotyledon in *Peperomia*, and their first leaf with the aerial organ of that form. He believes that monocotyly arose by division of labour between the cotyledons on account of adaptation to a geophilous habit, and the consequent necessity for an efficient absorbing organ within the seed. Its efficiency would be helped by the removal of all other embryonic structures from the seed as soon as possible after germination; consequently the rudimentary assimilating cotyledon, the plumule and radicle are carried down into the ground. Thus in course of time, one cotyledon may have become developed so as "to form a pseudo-terminal absorbent organ (Text-fig. 7, p. 420),

while the other cotyledon—the apparently lateral ‘first-leaf’—is left to develop from its rudiment outside the seed (cf. Text-figs. 8 and 9, p. 420)” (32, p. 422). Indeed, as Lotsy’s subdivisions of heterocotily suggest, this series may end in monocotyledonous cases, where the second aerial cotyledon is completely disguised as the first leaf (42, p. 624).

Further, Hill thinks it is possible that the median bundle of the single seed-leaf of some Monocotyledons has become divided in more advanced types, such as *Anemarrhena* (considered by Miss Sargent to be primitive), this being correlated with the parallel venation of the leaves of the Liliaceæ (32, p. 423). In opposition to Miss Sargent, he considers the type of anatomy in an *Arum* seedling as being more primitive and near dicotyledonous ancestors (such as Piperaceæ), and the *Anemarrhena* type as derived through such simpler Liliaceous forms as *Zygadenus*.

Lotsy is in complete agreement with Hill in regarding the Spadicifloræ as an example of heterocotily. As may be seen from his phylogenetic scheme (Diagram IV), he derives them from ancestors near the Piperales. Compton also apparently agrees with this view (11, p. 801)¹.

The second kind of heterocotily is that in which reduction or even complete suppression of one cotyledon has taken place.

Lotsy quotes as an example of reduction of one cotyledon the embryo of grasses, in which the scutellum functions as an ordinary suctorial cotyledon, while the epiblast is considered as representing the reduced second cotyledon. This view was put forward by Mirbel in 1810 (49, p. 424 in note), and some twenty years later, as we have seen, Agardh (1, p. 197) held that Grasses were the only true Monocotyledons because one cotyledon had become completely suppressed. As Compton points out in his recent paper (11, p. 800), it is unsafe to theorise about this case, for there still exists too great diversity of opinion as to the morphology of the grass embryo.

The chief supporter of the suppression theory is Henslow (30, 31), whose papers in 1892 and 1911 bring forward evidence, partly from experiments on land and water plants, in support of his contention which may be stated briefly as follows:—Monocotyledons and Dicotyledons come from a common dicotyledonous stock, members of which gave rise to true Dicotyledons or to Monocotyledons

¹ From a study of the morphology of germination, Gatin (24, p. 54) concludes that there is not sufficient evidence for the adoption or rejection of Hill’s theory.

according to their habitat on land or by, or in, water. The forms subjected to an aquatic or moist habitat became degenerate¹ owing to the weakening effect of water by saturating the protoplasm. This is shown in the case of division and fenestration of leaves of aquatic plants, loss of secondary growth by means of a cambium, and in the case of Monocotyledons, by complete loss of one cotyledon. Henslow maintains—apparently in answer to Miss Sargent's criticism that there is no evidence of suppression—that the second strand in the cotyledon of that author's so-called primitive Monocotyledons, is the last relic of the cotyledon which has been otherwise totally arrested (31, p. 743). After the aquatic Angiosperms had been subjected to weakening conditions through many generations, the effect of such conditions became fixed and hereditary, so that at the present time, Monocotyledons are unable to adapt themselves completely to land conditions in competition with the Dicotyledons—hence the retention of an aquatic habit by so many of them.²

In support of heterocotily, Compton (11, p. 802) quotes the case of *Ranunculus Ficaria*. It will be remembered that according to Miss Sargent (59, p. 75), this is a case of asymmetrical syncotily, or union of the cotyledonary petioles by one edge only (see also Sterckx, 66, p. 42). But according to Compton, the balance of evidence—such as vascular anatomy and venation of the cotyledonary blades—is in favour of the view of Hegelmaier (29) and Schmid (63, p. 211) that the seed-leaf in *Ranunculus Ficaria* is a single organ. The evidence applies to *Corydalis* spp., *Carum Bulbocastanum*, *Pinguicula* spp., *Abronia* spp. Compton concludes that in these cases it is difficult to decide whether complete suppression of one cotyledon accounts for heterocotily, or whether the missing cotyledon has been retarded in development, and now appears as the first foliage leaf.

Lotsy (42, p. 624) broad-mindedly admits the origin of monocotily in any of the ways described by various writers. He thinks, however, that the case of syncotily is less well-established than that of heterocotily.³

¹ Cf. de Vries (16, p. 15), who insists on the degenerate nature of Monocotyledons.

² A comparison of Henslow's view of the origin of Monocotyledons with that of Miss Sargent, shows that, according to Henslow, the aquatic habitat is primarily the *cause* of the evolution of Monocotyledons; while according to Miss Sargent, it is largely the *result* of the development of a monocotyledonous condition.

³ Guillaumin (25, p. 232) also admits that monocotily may have arisen by fusion of two cotyledons, or by suppression of one.

V. CONCLUSION.

From the foregoing review it will be seen that there is very great diversity of opinion concerning the cause and manner of development of the Monocotyledons, while their immediate ancestry, though generally thought to be dicotyledonous, is still a matter for discussion. The speculations for which Arber and Parkin (2, 3) have been largely responsible, concerning their more remote ancestry, have little more than a theoretical value.¹ They are intensely interesting, and are within the bounds of possibility, but in the present state of our knowledge, they are somewhat daring. The gap between Gymnosperms and Angiosperms is still waiting to be filled by discoveries as important as those of Pteridosperms and Bennettitales.

¹ See Oliver (53) ; Scott (64, p. 658) ; Lignier (38) ; Coulter and Chamberlain (12, p. 280)

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APPENDIX.

SINCE the above review was written three important papers dealing with the origin of Monocotyledons have appeared.

The first of these is concerned with the point of contact between the Monocotyledons and the Dicotyledons. Nitzschke (3) maintains that, owing to its position, the embryo-sac is less likely to become affected by external (ecological and physiological) conditions than other plant organs. He accordingly has investigated and compared the developmental history of the embryo-sacs of the apocarpous nymphæaceæ—*Cabomba* and *Brasenia*—and those of certain forms of the Helobieæ, particularly of Butomaceæ and Alismataceæ. He finds that of all Ranalean types investigated by him or by other authors, the apocarpous nymphæaceæ show the greatest similarity, so far as embryo-sac development is concerned, to the Helobieæ. His conclusion is, therefore, that they may have been derived from a common ancestor.

The other two papers deal with the origin of the monocotyledonous condition.

Miss Farrell (2), working on the ovary and embryo of *Cyrtanthus sanguineus*, concludes that the sheath of monocotyledons is probably the result of fusion of two or more cotyledons. In this species, the youngest observed stages of the embryo, show the stem-tip surrounded by a four-lobed sheath; the growth of this sheath (1, p. 516) produces the cotyledonary ring in which the four lobes or growing points persist for a time, but ultimately grow together in pairs producing two cotyledonary rudiments. Finally the cells of one of the cotyledons cease to divide, and an apparently single terminal cotyledon results. Miss Farrell considers her investigation to furnish a last proof of the theory of the derivation of monocotly from dicotly.

The work of Coulter and Land (1) on *Agapanthus umbellatus* is in agreement with that of Miss Farrell with regard to the origin of the cotyledonary sheath. Their observations form the basis of a new theory of the origin of monocotly. *Agapanthus umbellatus* may produce monocotyledonous or dicotyledonous embryos, and in either case, the cotyledons arise as lateral structures from a peripheral zone surrounding the stem-apex of the proembryo. The proembryo is massive, a condition which Coulter and Land consider to be primitive for Angiosperms, and at its broad, somewhat flattened shoot-end the meristemic activity of the peripheral cells produces the cotyledonary zone, in which two or more growing points appear. By continued growth of the whole zone a sheath is formed surrounding the depressed stem-apex, and equal growth of the two primordia produces a dicotyledonous embryo. In other cases, however, only one growing-point continues to divide, so that apparently only one cotyledon is developed. Coulter and Land maintain that, since the sheath and the cotyledons are all one structure, the production of a so-called single cotyledon is due to the "growth of the whole cotyledonary zone under the guidance of a single growing point" (1, p. 515), instead of the distribution of activity between two separate primordia. In polycotly, more than two primordia appear and persist in growth. The authors compare the zonal development of the cotyledonary sheath with its varying number of growing points, with the zonal development of symmetrical corollas, which according to them, provides a parallel case.

In view of the importance attached by Miss Sargent and other

workers to the vascular anatomy of seedlings, it may be noted that Coulter and Land consider the vascular strands to be secondary structures, the position and appearance of which are determined by the position of the growing points. They cannot therefore be regarded as phylogenetically important structures.

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